

FOSSIL LIZARDS FROM THE PLIOCENE CHINCHILLA LOCAL FAUNA, QUEENSLAND, WITH DESCRIPTION OF A NEW SPECIES

MN HUTCHINSON & BS MACKNESS

HUTCHINSON, MN & MACKNESS, BS. 2002. Fossil lizards from the Pliocene Chinchilla Local Fauna, Queensland, with a description of a new species. *Records of the South Australian Museum* 35(2): 169–184.

The lizard fauna of the Middle Pliocene Chinchilla Local Fauna consists of members of the Gekkonidae, Agamidae, Varanidae and Scincidae. A new species of the scincid lizard genus *Tiliqua* is described, based on a complete right dentary. The new species combines relatively unspecialised dentition, most similar to that of *T. nigrolutea*, with large size and relatively gracile proportions, with a relatively slender coronoid process and deeply concave margin between the coronoid and angular processes. An additional scincid dentary is probably referable to the genus *Cyclodomorphus*. Cranial remains of a species of the gekkonid genus *Diplodactylus* are described, representing a group of species within *Diplodactylus* that have a vestigial jugal. An agamid dentary and two varanids of differing sizes are also described.

Mark N Hutchinson, Department of Herpetology, South Australian Museum, North Terrace, Adelaide, South Australia 5000. Brian S Mackness*, School of Biological Sciences, University of New South Wales, Kensington, New South Wales 2052. *Current address: PO Box 560, Beerwah, Queensland 4519, Australia. Manuscript received 17 April 2002.

The Chinchilla Sand was named by Woods (1960) for a sequence of weakly consolidated grey to yellowish and light brown sands, ferruginised heterogeneous conglomerates, grits, sandy clay and clays. These outcrops range from shallow beds to sections several metres deep along a 40 km stretch of the Condamine River valley, approximately 240 km ENE of Brisbane.

The Chinchilla Sand has yielded a diverse array of fossil remains, the Chinchilla Local Fauna (Mackness, Wilkinson & Wilkinson 1999). Mammals have been the best studied group and the fauna recovered comprises macropodids (Bartholomai 1963, 1966, 1967, 1973, 1975, 1976; Flannery & Archer 1983), phascogaleids (Archer 1977), thylacoleonids (Archer & Dawson 1982; Bartholomai 1962; Woods 1956), peramelids (Mackness et al 2000), dasyurids (Archer 1982; Bartholomai 1971; Dawson 1982; Wroe & Mackness 1998, 2000a, 2000b), a thylacine (Mackness et al submitted), murid rodents (Godthelp 1990) and a molossid bat (Hand et al 1999). At least three lineages of birds are also known, an emu, a rail and a duck (Olson 1975, 1977; Patterson & Rich 1987). The living lungfish *Neoceratodus* and platysid catfish have also been recorded (Kemp & Molnar 1981; Mackness et al 1999). Reptile remains described so far pertain to larger taxa, such as crocodilians

(*Palimnarchus*), turtles and madtsoiid snakes (Bartholomai & Woods 1976; Gaffney 1981; Gaffney & Bartholomai 1979; Mackness & Scanlon 1998; Woods 1960, 1962). The only lizards to date have been Hecht's (1975) identification of a number of large varanid fossils from the Chinchilla Local Fauna as *Megalania* sp.

The Chinchilla Local Fauna appears to biocorrelate with the Kanunka Local Fauna of the Tirari Desert, South Australia (Tedford et al 1992) and the Spring Park, Bow and Big Sink Local Faunas (Mackness et al 2000). On the basis of the Kanunka Local Fauna having a magnetostratigraphic age of approximately 3.4 million years, the Chinchilla Local Fauna is estimated to be between late Early Pliocene and Middle Pliocene in age (Tedford et al 1992).

Lizard fossil remains have received relatively little attention in reports on Australian fossil faunas, due both to a paucity of material and a lack of data concerning osteology. In some lineages of lizards, such as agamids (Covacevich et al 1990) and varanids (Mackness & Hutchinson 2000), the restricted amount of morphological divergence within the living fauna makes identification problematic. For the anatomically diverse skinks and gekkonoids, this picture is steadily changing for the better as new finds focus attention on specific areas of anatomy. In this

study we point out some useful character states of gekkonid skulls that permit attribution to both major lineages and more restricted species groups. We also build on the knowledge of one of Australia's most characteristic lizard faunal elements, the bluetongue skinks of the genus *Tiliqua* (Shea & Hutchinson 1992) to describe a new and distinctive species.

MATERIALS AND METHODS

The specimens described here were recovered through quarrying or wet sieving of sediments from 'Wilkinson's Quarry', Chinchilla, Queensland, a site that has been continuously worked by Cec and Doris Wilkinson for over 11 years. The sediments are primarily fluvial in nature and represent a number of depositional events. Most fossils in these units occur as isolated pieces and all represent Pliocene taxa (Mackness, Wilkinson & Wilkinson 1999).

Specimens were examined using a Wild M3Z stereomicroscope with eyepiece micrometer and drawing tube. The fossils are registered in the collection of the Queensland Museum, Brisbane and were compared with skeletal material in the collection of the South Australian and Western Australian Museums. Comparative scincid specimens included all living species of *Tiliqua* and representatives from all species groups in the genera *Cyclodomorphus* and *Egernia*. The morphology of the gekkonid fossils dictated the gekkonid specimens that would be the most likely candidates for comparison, the 'unspecialised' small- to medium-sized diplodactylines. We also examined representatives of those genera of gekkonines that occur in the Australian region and the adjacent Melanesian-Indonesian region, as well as a scattering of specimens from across the global diversity of the subfamily Gekkoninae. In addition, published diagrams and discussions of gekkonid cranial osteology were consulted to ensure that our selection was representative, mainly aimed at justifying some of the general statements we make regarding major patterns of variation that differentiate gekkonine and diplodactyline skulls and mandibles. Specimens examined are listed in Appendix 1. Terminology for bones follows Estes et al (1988).

Measurements

Measurements of varanid vertebrae and the large *Tiliqua* species were made using Vernier callipers accurate to 0.05 mm, while smaller

specimens and teeth were measured with a calibrated microscope eyepiece. Vertebral measurements are summarised below and largely follow Smith (1976). Statistical analyses of these measurements are provided in Appendix 2; Tables 1 and 2.

Vertebral length (Pr-Po) — the greatest distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis.

Vertebral width (Pr-Pr) — the maximum width of the vertebra between the lateral edges of the prezygapophyses.

Vertebral width (Po-Po) — the maximum width of the vertebra between the lateral edges of the postzygapophyses.

Centrum minimum width (BW) — the smallest distance across the centrum.

Condylar width (CW) — the greatest transverse diameter of the condyle.

Abbreviation for specimen numbers: AR: University of New South Wales Research Collection; SAM: South Australian Museum; WPC: Wilkinson Private Collection.

SYSTEMATICS

Order SQUAMATA Oppel, 1811

Family AGAMIDAE Gray, 1827

Unidentified material

Material examined

A left dentary (WPC 1354), bearing mid to rear section of tooth row.

Characters

Agamid reptiles are distinguished in having a dentition combining one to three anterior pleurodont teeth followed by acrodont teeth. Other agamid features are summarised by Estes (1983).

Description

The specimen is from a moderately sized individual, perhaps of skull length of approximately 30 mm, and bears nine acrodont teeth. The posterior of the dentary is largely missing although the facet for the coronoid is still visible. No mental foramina are discernible on the specimen.

Remarks

Covacevich et al (1990) discussed several problems in identifying fragmentary agamid remains beyond family level.

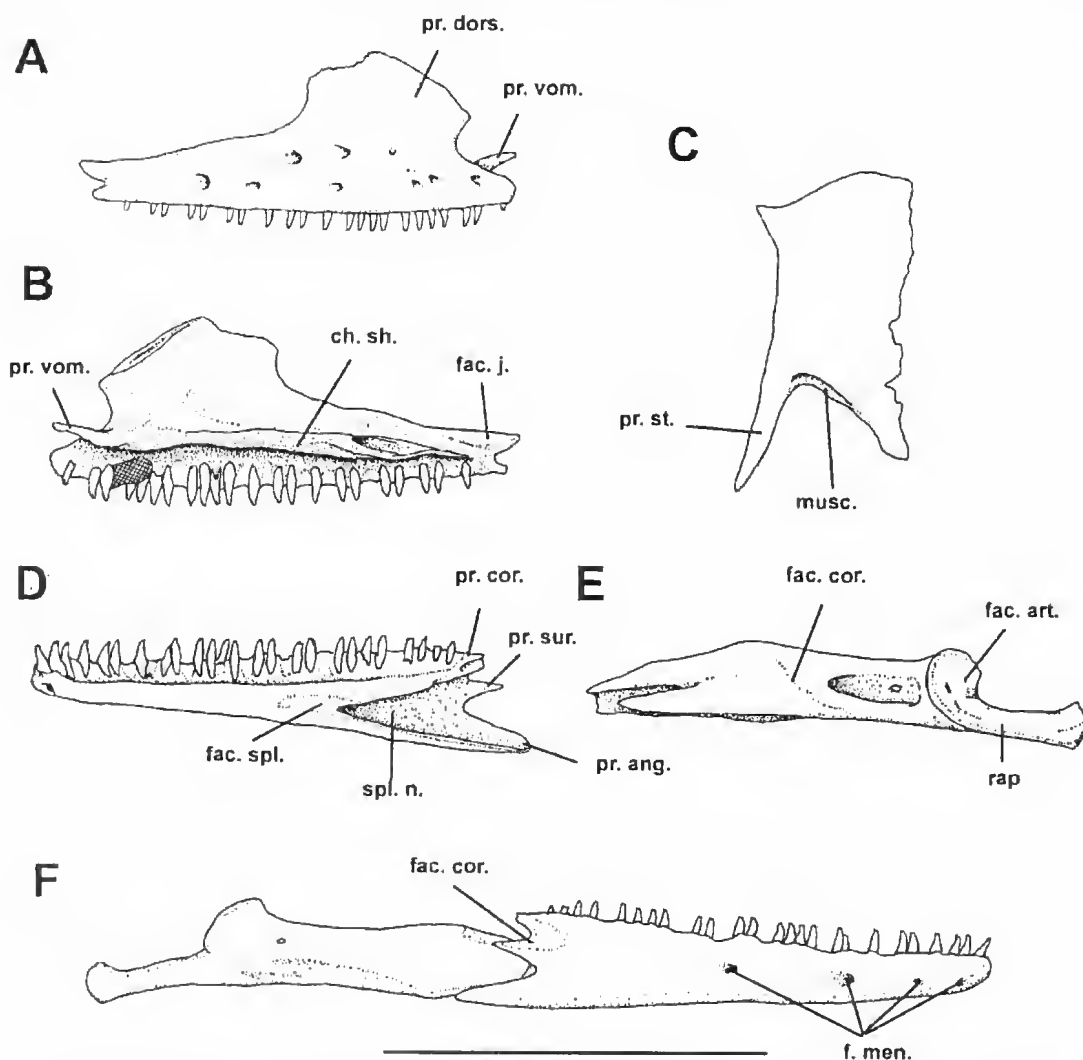


FIGURE 1. A–F *Diplodactylus cf. steindachneri*. A, right maxilla (QM F30573) in lateral view and B, medial view. C, left parietal (QM F30574) in dorsal view. D–F right mandible (QM F30572). D, lingual view of dentary. E, lingual view of articular + surangular. F, articulated mandible in labial view. Abbreviations: ch. sh. – choanal shelf; f. men. – mental foramina; fac. art. – articular facet; fac. cor. – coronoid facet; fac. j. – jugal facet; fac. spl. – splenial facet; musc. – insertion point for dorsal neck musculature; pr. ang. – angular process; pr. cor. – coronoid process; pr. dors. – dorsal process; pr. st. – supratemporal process; pr. sur. – surangular process; pr. vom. – vomerine process; rap – retroarticular process; spl. n. – splenial notch. Scale bar = 5 mm.

Family GEKKONIDAE Gray, 1825

Subfamily DIPLODACTYLINAE Underwood, 1954

Diplodactylus Gray, 1825

Diplodactylus cf. steindachneri
(Fig. 1A–F)

Material examined

Right maxilla (QM F30573); left parietal (QM F30574); partial right mandible (QM F30572), consisting of a dentary and fused surangular plus articular.

Description

Maxilla. The maxilla (QM F30573, Fig. 1A–B), a right element, is almost complete, with slight

erosion of the edges on the margin of the dorsal process. Total length 6.1 mm. A slender, dorsoventrally flattened vomerine process extends medially from the anteromedial end of the bone. The facial portion of the maxilla is gently arched along its dorsal margin. Although the dorsal margin is slightly damaged, there is no posterodorsally directed frontal process. The margin bordering the nasal opening is almost semicircular. The outer surface of the maxilla bears two series of foramina; one consisting of a row of six openings just above the teeth, the posteriormost the largest; and a second consisting of three relatively large openings at the level of the anteroventral corner of the orbit. The subocular ramus of the maxilla is robust and relatively short and deep. It does not taper to a point, as is usual in gekkonoids; the outline of the caudal extremity of the specimen is bifurcated, with the dorsal fork larger than the ventral. The internal surface of the maxilla bears a prominent choanal shelf, which is constricted at its mid-point and again anteriorly before projecting as the vomerine process. The inner face of the suborbital region has a small facet for a vestigial jugal on the dorsal fork, below which is a longer facet for the ectopterygoid.

There are 33 tooth loci, most with intact teeth. The teeth are small, cylindrical in section and tapering to acute points, with an apical cusp and lingual cusp separated by a narrow occlusal groove; this morphology is regarded as typical and plesiomorphic for gekkonoids (Sumida & Murphy 1987). The individual teeth are uniform in size and vary only slightly in shape.

Parietal. The left parietal (QM F30574) (Fig. 1C) is complete except for slight erosion along the medial margin. In common with many living species, the medial edge of the bone may not have been fully ossified. Beginning at the bone's anteromedial apex, the anterior margin describes a shallow sinusoidal curve posterolaterally, terminating at the obtusely pointed apex of the articulation point with the postorbital. The caudal margin of the body of the parietal is almost straight-edged and faces caudolaterally. This margin bears a shallow caudally opening pocket, which would have been the insertion point for the superficial neck musculature. The supratemporal process is relatively slender and tapers to an acute point. Ventrally, the bone bears a descending flange parallel to the lateral margin, the flange descending to a pointed projection (epipterygoid process) about halfway along. Overall length of the specimen is 4.2 mm;

width (measured at the apex of the postorbital articulation) 1.9 mm.

Adult mandible (QM F30572, Fig. 1D–F) is represented by a complete dentary and nearly complete compound bone consisting of the fused articular and surangular bones. The angular, splenial (or the composite angulosplenial typical of diplodactylines) and coronoid are absent.

Dentary. Total length (taken as a straight line from symphysis to tip of angular process) 6.5 mm. There are 36 teeth or tooth loci, the teeth being similar in size and shape to those on the maxilla, with the most anterior teeth having somewhat more recurved tips.

The dental sulcus is well defined by a lingual parapet that is evident as far as the posteriormost tooth. The posterior limit of the bone has three processes, which define two embayments. The uppermost (coronoid) process terminates just behind the last tooth and has facets on its lingual and labial aspects for the coronoid bone. The middle (surangular) and lower (angular) processes would have terminated at about the level of the apex of the dorsal process of the coronoid bone. The labial face bears four mental foramina, the posteriormost lying at the level of the 24th tooth. On the lingual face, the splenial notch extends forward to the level of the 27th tooth, and there is a facet extending anteriorly to the notch, suggesting that the splenial terminated at about the level of the 22nd tooth. There is no bony intramandibular septum exposed within the splenial notch.

Comparisons

The identification of these specimens as gekkonoids is based on several characters that are uniquely combined in this clade. The morphology of the articular and retroarticular region of the mandible shows an articular facet facing posterodorsally and the retroarticular process as slender and ventrally positioned. There is complete overgrowth by the dentary of the groove for Meckel's cartilage. The teeth are small, finely pointed and numerous. The parietal is poorly ossified, paired and lacks a pineal foramen. The elements are those of a small (approx 45 mm SVL) generalised gecko.

Studies of the phylogenetic relationships among the Gekkota (Bauer 1990; Donnellan et al 1999; Estes et al 1988; Kluge 1967a, 1967b, 1987) agree that the Australian region has three of the four major gekkotan lineages: the Gekkoninae, Diplodactylinae and Pygopodidae. The remaining gekkotan clade, the Eublepharidae, is found no

closer than Borneo (the genus *Aelurascalabotes*). To further establish the affinities of the Chinchilla specimens, we have noted several characters that appear to be useful in diagnosing membership of particular gekkotan lineages, based on the most commonly recovered elements: mandibles, maxillae, frontals and parietals.

Maxilla. The shape of the maxilla differs markedly between most gekkonines and the rest of the gekkotan lineages. Authors describing this area of the face generally emphasise bony contacts, using the dichotomy of either a prefrontal–nasal contact (shown by most diplodactylines) or a frontal–maxilla contact (shown by most gekkonines) (Fig. 2). In most Australian gekkonines (*Cyrtodactylus*, *Gehyra*, *Heteronotia*, *Nactus*), and in most other gekkonines examined, the maxilla arches posteromedially to contact the frontal, terminating in a frontal process that greatly reduces the exposure of the prefrontal and excludes the prefrontal from the nasal. In the remaining Australian gekkonine *Christinus* and in

diplodactylines, the maxilla lacks this frontal process and the prefrontal includes an anteromedial process that contacts the nasal, usually excluding it from the maxilla. In eublepharids (*Aelurascalabotes* [Grismer 1988], *Hemitheconyx* [Rieppel 1984]) the prefrontals bear anteromedial processes but they are excluded from the maxilla due to well-developed anterolateral processes of the frontal; the maxilla is similar in shape to that of the diplodactylines. Pygopods are variable but most tend to show a gekkonine-like posterodorsal expansion of the maxilla to contact the frontal. The maxilla of the Chinchilla gecko has a low, gently arched dorsal process with no frontal process.

The Chinchilla fossil shows a distinctive feature of the maxilla that suggests a particular relationship within the Diplodactylinae. In lateral view its subocular ramus shows a relatively deep, bifurcate posterior termination, a characteristic also seen in a few species of the genus *Diplodactylus*. In these species the notched tip of the terminal portion of the maxilla is correlated

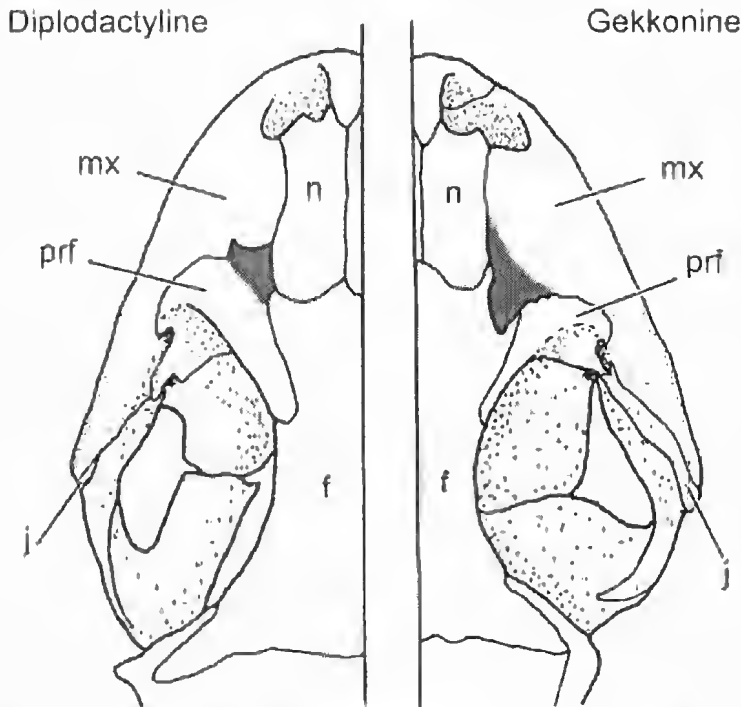


FIGURE 2. Comparison of the anterior part of the skull in a diplodactyline (*Diplodactylus stenodactylus*) and an Australian gekkonine (*Gehyra dubia*) gecko showing the usual patterns of contact between the frontal (f), nasal (n), maxilla (mx) and prefrontal (prf) bones. Areas in grey show the anteromedial (nasal) process of the prefrontal (diplodactyline), and the frontal process of the maxilla (gekkonine). *D. stenodactylus* also shows a vestigial jugal (j), compared with the usual degree of development of this bone in most other gekkotans as shown by *G. dubia*.

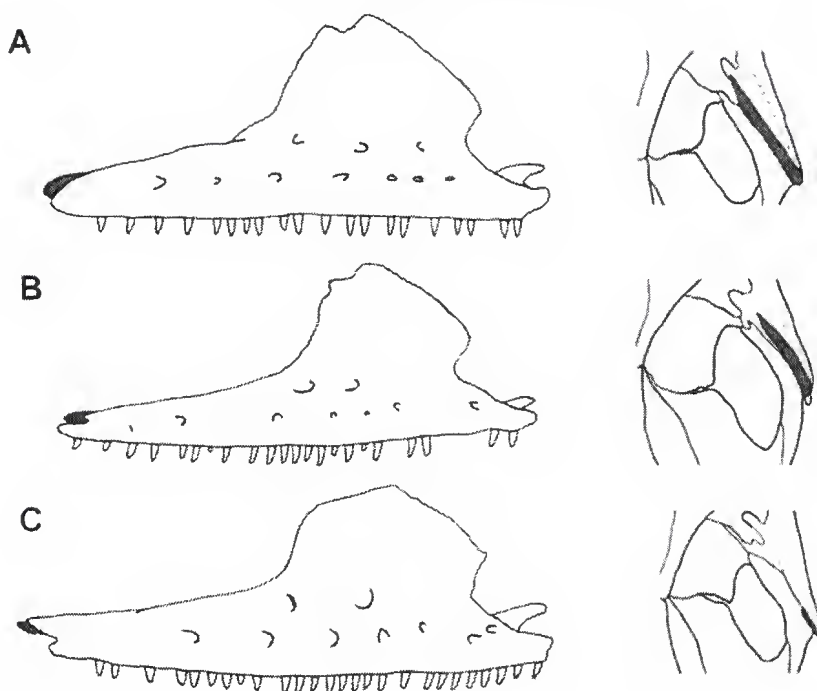


FIGURE 3. Right maxilla (slightly anterodorsal in aspect) and sketch of dorsal view of right orbit in three species of *Diplodactylus*, showing reduction of the jugal (grey), A, *D. granariensis* (R29135); B, *D. damaeus* (R24553); and C, *D. steindachneri* (R05153). Approx. length of maxillae 6–7 mm, not to scale.

with reduction of the jugal bone reported by Kluge (1967b). The two species reported as having the greatest reduction of the jugal (*D. steindachneri* and *D. stenodactylus*) have the most pronounced development of the bifurcate shape (Fig. 3A–C) and are essentially identical in appearance to the Chinchilla maxilla.

Frontal. No frontal has been recovered at Chinchilla, but future finds should be identifiable as gekkonine if there are three facets on its anterior portion (for the nasal, maxilla and prefrontal) or otherwise if there are only two facets. The relatively long nasal processes of eublepharid frontals might also be diagnostic for that clade.

Parietal. Many gekkotan taxa have distinctive parietal morphologies. However, this bone shows marked ontogenetic variation in its degree of ossification, the elaboration of muscle attachment points on its lateral and posterior margins, and the robustness of the supratemporal process. The most distinctive feature of the Chinchilla specimen is the concavity for the neck musculature on the posterior margin. This arrangement is not typical

of most gekkos, where the musculature simply attaches to the posterodorsal surface and edge of the parietal, or to the posteroventrally deflected trailing edge, generally with no more than a depression or a low ridge to mark the point of attachment. A more-or-less well-defined pocket is present in some members of the genus *Diplodactylus* (*D. stenodactylus*, *D. steindachneri*, *D. byrnei*, intraspecifically variable in *D. damaeus*) but is absent from other Diplodactylinae examined and was not seen in the gekkonines. Pygopod parietals are much slenderer than those of other gekkotans, the midline length being at least twice the width (cf less than 1.5 times the width).

Mandible. Some diplodactyline and gekkonine taxa as well as pygopods (Hutchinson 1997) have unique modifications of the mandible that are diagnostic for individual genera, but many gekkotan taxa have mandibles that are superficially similar in overall shape. In these generalised mandibles, the retroarticular process provides a key to the two major gecko subfamilies. In gekkonines, the retroarticular

process is generally spoon-like in shape, its dorsal surface forming an obvious, concave bowl. In most diplodactylines (*Saltuarius* and some *Strophurus* are exceptions) and in pygopodids, the retroarticular process is rod-like, with an oval, flattened or shallowly concave cross-section and terminated by a club. The morphology of the dorsal surface of the retroarticular process in eublepharids has not been described (published diagrams show only the shape in lateral or ventral view). The Chinchilla specimen has the clubbed, diplodactyline type of retroarticular process.

The fossil maxilla and mandible therefore not only show an overall similarity with diplodactylines, but also share several discrete character states that indicate specific diplodactyline affinities. The characteristics that distinguish the fossils are those that are uniquely combined in the genus *Diplodactylus*.

The Chinchilla fossils were found as disarticulated elements but their size and preservation, especially the mandible and maxilla, are consistent with having come from one animal. Based on the possession of a bifurcate terminus to

the posterior ramus of the maxilla and the presence of a 'pocket' on the trailing edge of the parietal, they are referred to *D. steindachneri*. It is one of three species of *Diplodactylus* still found in the region (the other two are *D. vittatus* and *D. tessellatus*, Ingram & Raven 1991), and is the only one of these three species to have a vestigial jugal and bifurcate maxillary terminus. The other species with reduced jugals, members of the *D. stenodactylus* group, are found in the deserts of central and western Australia, the closest to Chinchilla being *D. immaculatus* of western Queensland.

Family SCINCIDAE Gray, 1825

Subfamily LYGOSOMINAE Mittleman, 1952

Tiliqua Gray, 1825

Tiliqua wilkinsonorum sp. nov. (Fig. 4A–B)

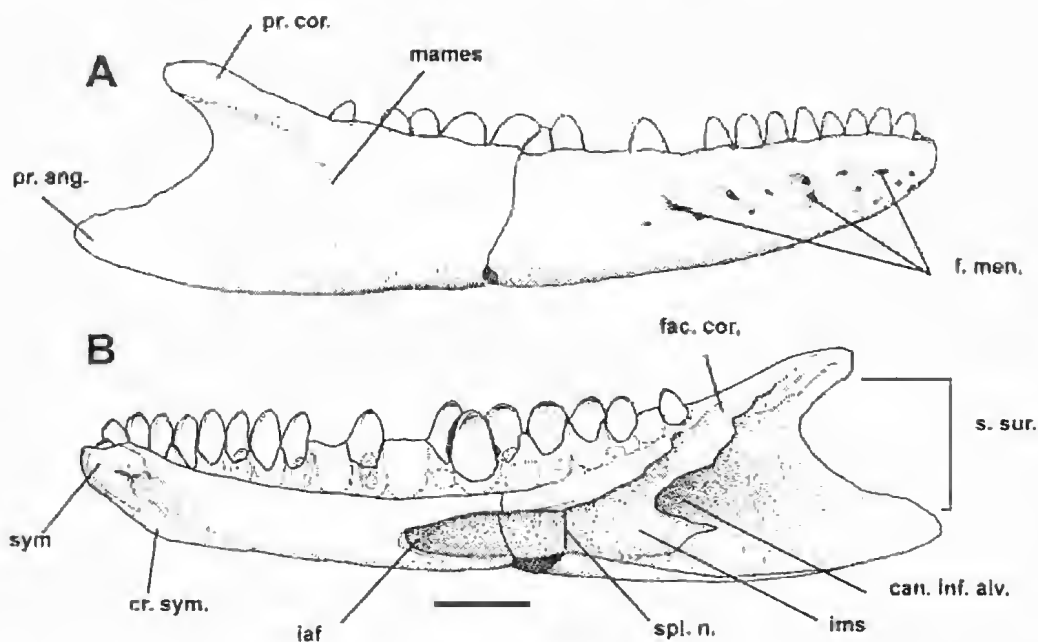


FIGURE 4. A–B *Tiliqua wilkinsonorum* n. sp. QM F30567 Holotype right dentary. A, labial; B, lingual. Abbreviations: can. inf. alv. – inferior alveolar canal; cr. sym. – symphyseal crest; f. men. – mental foramina; fac. cor. – coronoid facet; iaf – inferior alveolar foramen (= anterior inferior alveolar foramen); ims – intramandibular septum; mames – limits of attachment for external adductor musculature; pr. ang. – angular process; pr. cor. – coronoid process; spl. n. – splenial notch; s. sur. – surangular suture; sym. – symphysis. Scale bar = 5 mm.

Material examined

Holotype: a right dentary (QM F30567).

Type Locality

Wilkinson's Quarry site, Chinchilla area, southeastern Queensland. The specimen comes from a fossil-bearing unit within the quarry that lies unconformably on top of a layer of fine sand. The sediments are primarily fluvial in nature and represent a number of depositional events.

Age

Chinchilla Local Fauna, late Early to Middle Pliocene (Tedford et al 1992).

Diagnosis

A large species, dentary tooth row length 33 mm, differing from other *Tiliqua* by the following combination of characters: all tooth crowns pointed and retaining an occlusal ridge, the crown scarcely wider than the shaft; coronoid process of the dentary relatively slender, narrower than long, its shape correlated with a curved and concave, rather than angular or straight, dentary-surangular suture connecting the base of the coronoid process with the tip of the angular process.

Description

A right dentary, bearing a complete row of 20 teeth or tooth loci. The specimen is almost intact, being slightly damaged at the apex of the splenial notch and on the ventral edge adjacent to a repaired crack through the jaw at the level of the 15th tooth. Total length, from the anteriormost point of the symphysis to the tip of the angular process, 47.8 mm. Depth at level of 16th tooth (excluding tooth), 7.8 mm. Maximum depth of jaw, measured vertically from the apex of the coronoid process, 13.1 mm. Maximum width, measured in occlusal view at the level of the 16th tooth, 8.0 mm.

Meckelian groove closed, no trace of suture. A pronounced crest runs caudally from the symphysis along the ventrolingual margin of the jaw, gradually merging with the body of the dentary at about the level of the eighth tooth. Apex of the splenial notch at about the level of the 12th or 13th tooth, slight uncertainty due to the broken edge of the inferior alveolar foramen at the apex of the notch. Labial surface with pronounced, arcuate adductor muscle scar that has its apex level with the last tooth. Angular process projects 15 mm beyond the level of the last tooth. Dorsal margin of angular process merges with the

ventral margin of the coronoid process along a smooth concave curve that has its apex at the level of the tooth row. Coronoid process well developed, flattened, but relatively small compared with other *Tiliqua*. A series of mental foramina starts at the level of the 11th tooth and runs anteriorly to the symphysis. These foramina are mostly arranged as a series of superposed pairs, with a total of about nine in the series.

Intramandibular septum fused ventrally along its length to the ventral lamina of the dentary, completely separating the inferior alveolar canal from the Meckelian canal. Caudal margin of intramandibular septum with a deep, curved notch, bounded ventrally by a caudally projecting prong.

Tooth row, in occlusal view, almost straight, gently curving medially anterior to the level of the sixth tooth. Labial wall of dental sulcus tall and robust. Lingual wall low but distinct anteriorly, reducing caudally and disappearing by about the level of the 16th tooth. Lingual face of dentary below the dental sulcus vertical, sharply distinct from the tooth row. Dentition pleurodont. The first of 20 teeth is broken off and the 10th, 12th and 19th loci are empty, but all other teeth are present and well preserved. The teeth vary distinctly in size, becoming larger progressing caudally, with the maximum reached in positions 13 to 16, the subsequent teeth then diminishing in size. As a guide to the changes in tooth size, tooth 6 is 3.5 mm high by 1.3 mm wide (measured normal to the lingual aspect) while tooth 14 is 4.3 mm high by 2.4 mm wide; thus, height increases by 23% and width by 85%. In lingual view, the tooth crowns are acutely pointed anteriorly, becoming obtusely pointed by about the 13th tooth. The crown of each tooth is margined by an occlusal ridge that separates its lingual and labial surfaces. In mesial view the tooth crowns have a parabolic curved outline labially, but the lingual surface is flatter, descending almost vertically from the apical ridge and forming an angular contact with the rounded labial surface. On the largest teeth, several low striae run vertically down from the apical ridge on both labial and lingual surfaces of the crown.

Comparisons

The combination of the closed Meckelian groove, enlarged 'cheek' teeth with more than one large tooth posterior to position 10, and an enlarged and flattened coronoid process is unique and diagnostic for the bluetongue lizards of the genus *Tiliqua* (Shea 1990). The related genus

Cyclodomorphus has only a single enlarged cheek tooth, while other lygosomines with a closed Meckelian groove lack such obvious dental differentiation.

Most species of *Tiliqua*, however, have a more specialised dentition than *T. wilkinsonorum*. The plesiomorphic tooth crown morphology in skinks includes a convex outer surface, curving occlusally to a pair of apical ridges separated by a groove (M. H. pers. obs.; Sumida & Murphy 1987), while the lingual surface is flattened and oriented almost vertically, forming an angular contact with the apical ridge. In lingual and mesial views the crown is acutely pointed. In contrast to this, species of *Cyclodomorphus* and *Tiliqua* have teeth modified for durophagy (Estes & Williams 1984). Most species of *Tiliqua*, including *T. gigas*, *T. multifasciata*, *T. occipitalis*, *T. pusilla*, *T. rugosa* and *T. scincoides*, have cheek teeth with expanded crowns, and have lost or greatly reduced the plesiomorphic asymmetry of the crown. In occlusal view the crown is circular in shape, and when viewed mesiodistally the crown profile, a convex curve, is similar in shape lingually and labially. The apex of the tooth has a central conical projection with pronounced striae radiating over the crown from this central point. Most individuals lack an occlusal ridge, although many *T. occipitalis* and some *T. rugosa* have a remnant on the tooth apex. *Tiliqua adelaidensis* has quite different dentition in which the enlarged cheek teeth are labiolingually compressed, with a pronounced cutting edge formed by the apical ridge. *Tiliqua nigrolutea* is the living species that shows the closest dental similarity to *T. wilkinsonorum*. The teeth show little expansion of the crowns, which are pointed and retain an obvious occlusal ridge that demarcates the crown into lingual and labial aspects. These two species show an asymmetric tooth crown profile in mesiodistal view, with a more steeply descending lingual surface. Compared with *T. nigrolutea*, the teeth of *T. wilkinsonorum* differ only in being more robust and having the crowns of the largest teeth more expanded and obtusely pointed. These differences could be attributed to allometry or individual variation in tooth proportions, which is considerable in living *Tiliqua* (M. H. pers. obs.). However, other characteristics of the fossil specimen differentiate it from both *T. nigrolutea* and other *Tiliqua* species.

The dentary is from a very large *Tiliqua*. Using the average ratio of tooth row to mandible length (0.48) that applies in extant *Tiliqua*, the tooth row length of *T. wilkinsonorum* of 33 mm extrapolates

to an approximate mandible length of 68 mm. This size is approached only by the largest males of *T. rugosa* and *T. scincoides* (G. M. Shea pers. comm.) and suggests that *T. wilkinsonorum* may have had a snout-vent length close to 400 mm and a mass in excess of one kilogram. In spite of this size, the dentary of *T. wilkinsonorum* is notably gracile. This is most clearly seen in the shape of the coronoid process and the surangular suture running from the base of the coronoid process to the tip of the angular process. In all extant *Tiliqua*, the coronoid process is dorsally and caudally expanded. This expansion is masked to some extent because the base of the coronoid process is absorbed by caudal expansion of the trailing edge of the dentary such that the surangular suture is not deeply incised into the labial lamina of the dentary. The precise course of this suture varies both inter- and intraspecifically (Fig. 5A-I). In *T. nigrolutea*, *T. occipitalis* and *T. rugosa*, this suture usually runs vertically from the coronoid process and then angles caudoventrally to the tip of the angular process of the dentary. In *T. adelaidensis*, *T. gigas*, *T. multifasciata* and *T. scincoides*, the suture tends to run caudoventrally in an almost straight line from the base of the coronoid process. In none does it trace the excavated curve seen in *T. wilkinsonorum* (and other skinks). In *T. wilkinsonorum* the coronoid process is less expanded than in any extant species, with the possible exception of *T. gigas*, but is more clearly defined ventrally by the anterior sweep of the concave surangular suture. In living *Tiliqua* species, the expanded coronoid process and adjacent parts of the dentary increase the strength of this region of the mandible and increase the area of attachment for the jaw-closing tendon of the *m. adductor medius externus superficialis* (Haas 1973). The relative slenderness of the coronoid process and the concave surangular suture in *T. wilkinsonorum* are closer to the morphology seen in other skinks, including *Egernia*, the genus that probably includes the sister group of the *Tiliqua* lineage.

In summary, *T. wilkinsonorum* is one of the largest known specimens of *Tiliqua*, and has less specialised teeth than all but *T. nigrolutea* and a more slender (plesiomorphic) coronoid process of the dentary than all but *T. gigas*. The morphology of the teeth and the relative gracility of the caudal end of the dentary suggest that *T. wilkinsonorum* was not as specialised for durophagy as most other large *Tiliqua*.

Tiliqua wilkinsonorum is the third species of *Tiliqua* to be found in the Tertiary of Australia

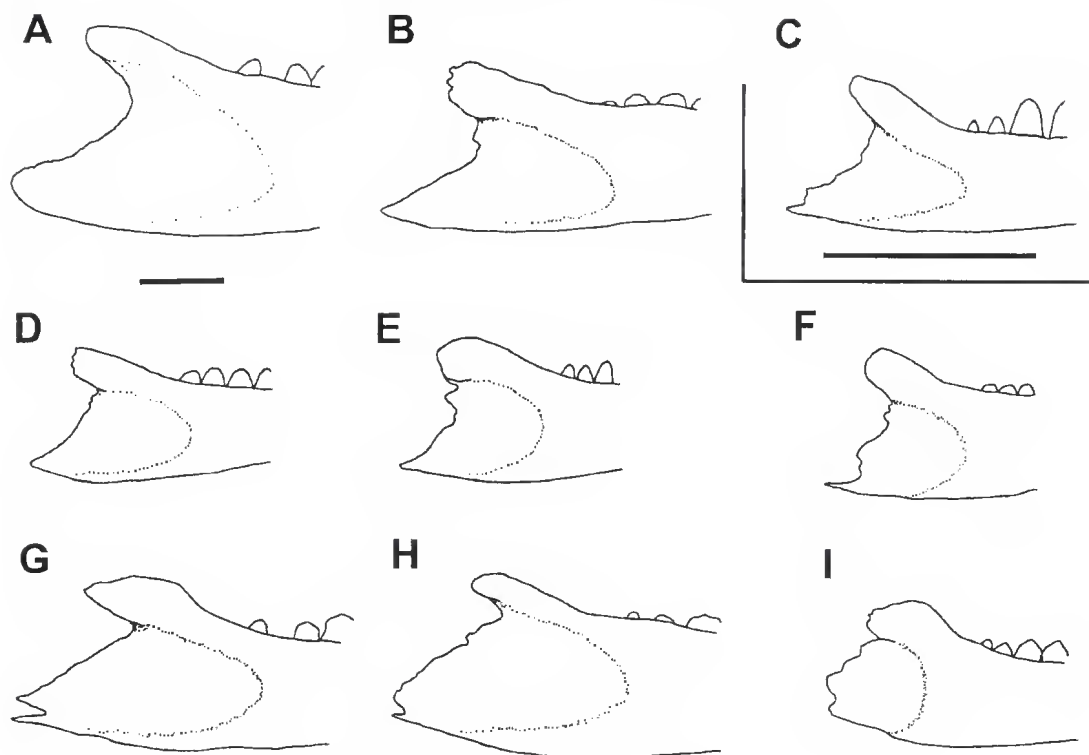


FIGURE 5. Dentary variation in *Tiliqua*. Detailed views showing variation evident in the degree of expansion of the coronoid process of the dentary and the shape of the dentary-surangular suture. All to same scale except *T. adelaidensis* (inset); both scale bars = 5 mm. A, *T. wilkinsonorum*. B, *T. rugosa* R27028. C, *T. adelaidensis* R40738. D, *T. nigrolutea* R02725. E, *T. nigrolutea* R47698. F, *T. occipitalis* R35758. G, *T. scincoides* R27039. H, *T. gigas* R11419. I, *T. multifasciata*, R35757.

and the second extinct species. Shea and Hutchinson (1992) described a very small species, *T. pusilla*, from the early Middle Miocene of Queensland, and specimens indistinguishable from a living species, *T. scincoides*, have been recorded from the Pliocene of South Australia (Pledge 1992) and Queensland (Mackness & Hutchinson 2000).

cf. *Cyclodomorphus* Fitzinger, 1843

Material examined

A partial dentary (QM F30568).

Description

The specimen represents about one-third of a left dentary, lacking the anterior portion, anterior to the last six teeth and lacking the coronoid and angular processes. It is not a juvenile, based on

several cycles of tooth replacement being evident. The groove for the Meckelian cartilage is completely obliterated by the dentary. The third-last tooth is markedly enlarged. The tooth anterior to this is absent, but its locus is smaller, while the other remaining teeth are smaller again. A single large mental foramen is present on the labial surface of the jaw at the level of the fourth-last tooth. The teeth, both enlarged and small, have blunt, slightly laterally compressed crowns with virtually no apical ornamentation such as cusps, grooves or striae.

Comparison

The fossil appears to have only one markedly enlarged cheek tooth, with a second moderately enlarged tooth anterior to it. Among extant Australian skinks, only members of the *Tiliqua* lineage combine a closed Meckelian groove and enlarged durophagous cheek teeth (Shea 1990).

The dentitions of the two genera of this lineage, *Tiliqua* and *Cyclodomorphus*, differ in that adults of *Tiliqua* have several enlarged cheek teeth while those of *Cyclodomorphus* usually have only one strongly enlarged tooth. On this basis as well as its small size and overall shape, the Chinchilla specimen is more similar to *Cyclodomorphus* than it is to *Tiliqua*. However, *Tiliqua adelaidensis* and the extinct *T. pusilla* show that the small species of *Tiliqua* may have only two enlarged cheek teeth, so that the distinction on tooth pattern alone is not entirely conclusive. Other attributes distinguishing the two genera, including the shape of the symphyseal region, are not preserved on the specimen. In the shape of the crowns and lack of occlusal striae, the fossil is unlike any species of either *Cyclodomorphus* or *Tiliqua* examined in this study, but it is too fragmentary to either allocate to a genus with certainty or to warrant description as a new taxon.

Family VARANIDAE Gray, 1827

?*Megalanina* sp.

Material examined

Five isolated dorsal vertebrae (WPC 115, 116, 2409, 2014, 3322), three isolated dorsal fragments (WPC 2040, 3555, 3556), four isolated caudal vertebrae (WPC, 1429, 1573, 2364, 2524).

Characters

The genus *Megalanina* is characterised in part by having massive thoracic and lumbar vertebrae with weakly developed zygosphenes (absent in typical *Varanus*) as well as small depressed neural canals. The adult teeth of *Megalanina* are large and slightly recurved distally. The anterior cutting edge is rounded and serrated distally. The posterior cutting edge is thin, blade-like and serrated along its entire length (Hecht 1975).

Description

The dorsal vertebrae are much more massive than those of any extant varanid but compare well in morphology with those from an extant varanid *Varanus varius* (AR 7641) as well as from large fossil varanids from the Bluff Downs Local Fauna (Appendix 2; Tables 1 and 2). The Chinchilla specimens are 62% larger than those measurements supplied for Australia's largest extant varanid, the perentie *Varanus giganteus* by Smith (1976) and 20% larger than those for the

large fossil varanid from Bluff Downs Local Fauna (Mackness & Hutchinson 2000).

Remarks

A single maxilla (QM F874) from the Chinchilla Sand was referred to *Varanus dirus* (Hecht 1975), a taxon originally described by De Vis (1889) on the basis of an isolated tooth from the Pleistocene Kings Creek locality. Hecht (1975) synonymised *V. dirus* with *Megalanina prisca*. Four isolated vertebrae (two caudals and two dorsals) have also been collected from the Chinchilla Sand and, although Hecht (1975) referred them to *Megalanina*, he also suggested that this material may represent a separate Pliocene species.

The assignment of the larger varanid vertebrae described in this paper to ?*Megalanina* is done purely on the basis of convention. Opinion is divided as to the current status of the genus, with Hecht (1975) and Molnar (1990) concluding it is valid but Estes (1983) and Lee (1996) suggesting that *Megalanina* should be synonymised with *Varanus*. A large collection of varanid fossils from Pliocene localities is presently under study by the authors.

Varanus sp.

Material examined

Two isolated dorsal vertebrae (WPC 118, 1430), one isolated caudal vertebra (WPC 3557).

Characters

These vertebrae are identified as varanid by their distinctive condyle-cotyle articulations. The dorsal vertebrae also show the characteristic constriction of the centra anterior to the condyle seen in *Varanus*.

Description

The vertebrae show characteristic varanid morphology with a range of centra lengths (Appendix 2; Table 3) that indicate a medium-sized goanna of the size of *Varanus gouldii*.

Remarks

Although Wilkinson (1995) suggests some characters for separating varanid species on the basis of vertebral morphology, many of these rely on the neural spine being present. This feature is missing on all three fossil vertebrae. Interspecific and/or intraspecific variation in varanid vertebrae have yet to be fully tested; therefore, characters

identified by Wilkinson (1995) must be used with caution.

DISCUSSION

The composition of the lizard fauna from the Chinchilla Sand Local Fauna, at least at family level (Appendix 2; Table 4), is similar to that of the Bluff Downs Local Fauna. This is the only other Australian Pliocene locality with a significant lizard record (Mackness & Hutchinson 2000). It differs from Bluff Downs in the generic representatives of each family, but the significance of this is unknown; it could merely be stochastic, reflecting the very small sample sizes at each locality. The palaeoenvironment was primarily fluvial for Chinchilla and lacustrine and fluvial for Bluff Downs.

The exact nature of the Chinchilla palaeoecology has yet to be determined. While there may have been a significant wetland component, as suggested by the presence of various aquatic taxa such as turtles (Gaffney 1981; Gaffney & Bartholomai 1979) and waterbirds (Olson 1975, 1977), there is also evidence that the environment was highly seasonal (Mackness et al 1999; Wroe & Mackness 2000). The presence of arboreal species such as *Koobor* (Archer 1977) and an unnamed phascolarctomorph (Mackness et al 1994) would be consistent with a complex and mature forest, but the composition of the mammalian fauna indicates a lack of undoubted

closed-forest species. Further, the predominance of grazing kangaroos and diprotodontids suggests that grasslands were also part of the environment.

The presence of an extinct reptile species at Chinchilla is noteworthy given the slow rate of faunal turnover in reptile populations (La Duke 1991). *Tiliqua wilkinsonorum* represents a distinctive but extinct species of lizard, a relatively uncommon observation for the Pliocene (Estes 1983). A conclusion that can be drawn from the presence of such 'fossil endemics' is that they signal ecological or geographical factors at Chinchilla during the Pliocene that are no longer present in recent environments.

ACKNOWLEDGMENTS

The authors thank Cec and Doris Wilkinson for their tireless efforts in recovering fossil remains from the Chinchilla Local Fauna over the past 12 years and for making the lizard material available for us to study. Glenn Shea, Jim Mead, Michael Archer and Suzanne Hand provided helpful comments on the manuscript. The study of the Chinchilla material was supported in part by an ARC Program Grant to M Archer; a grant from the Department of Arts, Sport, the Environment, Tourism and Territories to M Archer, S Hand and H Godthelp; a grant from the National Estate Program Grants Scheme to M Archer and A Bartholomai; and grants in aid to the Riversleigh Research Project from the University of New South Wales, Wang Australia Pty Ltd, ICI Australia and the Australian Geographic Society.

REFERENCES

- Archer, M. 1977. *Koobor notabilis* (de Vis), an unusual koala from the Pliocene Chinchilla Sand. *Memoirs of the Queensland Museum* 18: 31–35.
- Archer, M. 1982. Review of the dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. In M Archer (ed). 'Carnivorous Marsupials', vol. 2, pp. 397–443. Surrey Beatty & Sons: Chipping Norton, NSW.
- Archer, M & Dawson, L. 1982. Revision of the marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and thylacoleonid evolution in the late Cainozoic. In M Archer (ed). 'Carnivorous Marsupials', vol. 2, pp. 477–494. Surrey Beatty & Sons: Chipping Norton, NSW.
- Bartholomai, A. 1962. A new species of *Thylacoleo* and notes on some caudal vertebrae of *Palorchestes azael*. *Memoirs of the Queensland Museum* 14: 33–40.
- Bartholomai, A. 1963. Revision of the extinct macropodid genus *Sthenurus* Owen in Queensland. *Memoirs of the Queensland Museum* 14: 51–76.
- Bartholomai, A. 1966. The types specimens of some of de Vis' species of fossil Macropodidae. *Memoirs of the Queensland Museum* 14: 115–126.
- Bartholomai, A. 1967. *Troposodon*, a new genus of fossil Macropodinae (Marsupialia). *Memoirs of the Queensland Museum* 15: 21–33.
- Bartholomai, A. 1971. *Dasyurus dunmalli*, a new species of fossil marsupial (Dasyuridae) in the upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* 16: 19–26.
- Bartholomai, A. 1973. A genus *Protemnodon* Owen (Marsupialia: Macropodidae) in the upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* 16: 309–363.
- Bartholomai, A. 1975. A genus *Macropus* Shaw

- (Marsupialia: Macropodidae) in the upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* 17: 195–235.
- Bartholomai, A. 1976. A genus *Wallabia* Trouessart (Marsupialia: Macropodidae) in the Upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* 17: 373–377.
- Bartholomai, A. & Woods, J.T. 1976. Notes on the vertebrate fauna of the Chinchilla Sand. *Bulletin, Bureau of Mineral Resources, Geology and Geophysics, Australia* 166: 151–152.
- Bauer, A.M. 1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonner Zoologische Monographien* Nr 30: 1–218.
- Covacevich, J., Couper, P., Molnar, R.E., Witten, G. & Young, B. 1990. Miocene dragons from Riversleigh: new data on the history of the family Agamidae (Reptilia: Squamata) in Australia. *Memoirs of the Queensland Museum* 29: 339–360.
- Dawson, L. 1982. Taxonomic status of fossil devils (*Sarcophilus*, Dasyuridae, Marsupialia) from late Quaternary eastern Australian localities. In M. Archer (ed). 'Carnivorous Marsupials', vol. 2, pp. 517–525. Surrey Beatty & Sons: Chipping Norton, NSW.
- De Vis, C.W. 1889. On *Megalania* and its allies. *Proceedings of the Royal Society of Queensland* 6: 93–99.
- Donnellan, S.C., Hutchinson, M.N. & Saint, K.M. 1999. Molecular evidence for the phylogeny of Australian gekkonoid lizards. *Biological Journal of the Linnean Society* 67: 97–118.
- Estes, R. 1983. Sauria terrestria, Amphibia. In O. Kuhn & P. Wellenhofer (eds). 'Handbuch der Paläoherpetologie', Encyclopedia of Palaeoherpetology, pp 52–56. Gustav Fischer Verlag: Stuttgart.
- Estes, R., De Queiroz, K. & Gauthier, J. 1988. Phylogenetic relationships within the Squamata. In R. Estes & G. Pregill (eds). 'Phylogenetic relationships of the lizard families: Essays Commemorating Charles L. Camp', pp. 119–281. Stanford University Press: Stanford.
- Estes, R. & Williams, E.E. 1984. Ontogenetic variation in the molariform teeth of lizards. *Journal of Vertebrate Paleontology* 4: 96–107.
- Flannery, T.F. & Archer, M. 1983. Revision of the genus *Troposodon* Bartholomai (Macropodidae; Marsupialia). *Alcheringa* 7: 263–279.
- Gaffney, E.S. 1981. A review of the fossil turtles of Australia. *American Museum Novitates* 2720: 1–38.
- Gaffney, E.S. & Bartholomai, A. 1979. Fossil trionychids of Australia. *Journal of Paleontology* 53: 1354–1360.
- Godthelp, H. 1990. *Pseudomys vandykei*, a Tertiary murid from Australia. *Memoirs of the Queensland Museum* 28: 171–173.
- Grismer, L.L. 1988. Phylogeny, taxonomy, classification and biogeography of eublepharid geckos. In R. Estes & G. Pregill (eds). 'Phylogenetic relationships of the lizard families: Essays Commemorating Charles L. Camp', pp. 369–469. Stanford University Press: Stanford.
- Haas, G. 1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In C. Gans & T.S. Parsons (eds). 'Biology of the Reptilia', vol. 4, Morphology D, pp. 285–490. Academic Press: London.
- Hand, S.J., Mackness, B.S., Wilkinson, C.E. & Wilkinson, D.M. 1999. First Australian Pliocene molossid bat: *Mormopterus* (*Micronomus*) sp. from the Chinchilla Local Fauna, southeastern Queensland. *Records of the Western Australian Museum Supplement* 57: 291–298.
- Hecht, M. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proceedings of the Royal Society of Victoria* 87: 239–250.
- Hutchinson, M.N. 1997. The first fossil pygopod (Squamata, Gekkota) and a review of mandibular variation in living species. *Memoirs of the Queensland Museum* 41: 355–366.
- Ingram, G.J. & Raven, R.J. (eds) 1991. 'An Atlas of Queensland's Frogs, Reptiles, Birds and Mammals'. Queensland Museum: Brisbane.
- Kemp, A. & Molnar, R.E. 1981. *Neoceraodus forsteri* from the Lower Cretaceous of New South Wales. *Journal of Paleontology* 55: 211–217.
- Kluge, A.G. 1967a. Higher taxonomic categories of gekkonid lizards and their evolution. *Bulletin of the American Museum of Natural History* 135: 1–60.
- Kluge, A.G. 1967b. Systematics, phylogeny and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Australian Journal of Zoology* 15: 1007–1108.
- Kluge, A.G. 1987. Cladistic relationships in the Gekkonoidea (Squamata, Sauria). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 173: 1–54.
- La Duke, T.C. 1991. Fossil snakes of Pit 91, Rancho La Brea, California. *Los Angeles City Museum, Contributions to Science*. 424: 1–28.
- Lee, M. 1996. Possible affinities between *Varanus giganteus* and *Megalania prisca*. *Memoirs of the Queensland Museum* 39: 437–444.
- Mackness, B.S. & Hutchinson, M.N. 2000. Fossil lizards from the Early Pliocene Bluff Downs Local Fauna. *Transactions of the Royal Society of South Australia* 124: 17–30.
- Mackness, B.S., McNamara, G., Michna, P., Coleman, S. & Godthelp, H. 1994. The Spring Park Local Fauna, a new late Tertiary fossil assemblage from northern Australia. Abstracts of the Fourth Conference on

- Australasian Vertebrate Evolution, Palaeontology and Systematics. *Records of the South Australian Museum* 27: 223.
- Mackness, BS & Scanlon, JD. 1998. The first Pliocene record of the madtsoiid genus Scanlon, 1992 *Yurlunggur* from Queensland. *Memoirs of the Queensland Museum* 43: 783–785.
- Mackness, BS, Wilkinson, C & Wilkinson, D. 1999. The Chinchilla Local Fauna a new synopsis. *CAVEPS '99: Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*. Abstracts. Sydney, 6–7 April 1999.
- Mackness, BS, Wilkinson, C, Wilkinson, D, Emmott, A, Emmott, D & Wager, R. 1999. Fossil remains of a plotosid catfish from the Middle Pliocene Chinchilla Local Fauna and their palaeoecological implications. *CAVEPS '99: Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics*. Abstracts. Sydney, 6–7 April 1999.
- Mackness, BS, Wroe, S, Muirhead, J, Wilkinson, C & Wilkinson, D. 2000. First fossil bandicoot from the Pliocene Chinchilla Local Fauna. *Australian Mammalogy* 22: 133–136.
- Mackness, BS, Wroe, S, Wilkinson, C & Wilkinson, D. submitted. Pliocene distribution of the marsupicarnivore *Thylacinus* in Australasia. *Australian Mammalogy*.
- Molnar, RE. 1990. New cranial elements of a giant varanid from Queensland. *Memoirs of the Queensland Museum* 29: 232.
- Olson, SL. 1975. The fossil rails of C.W. de Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland. *Emu* 75: 49–54.
- Olson, SL. 1977. The identity of the fossil ducks described from Australia by C.W. de Vis. *Emu* 77: 127–131.
- Patterson, C & Rich, PV. 1987. The fossil history of the emus, *Dromaius* (Aves: Dromaiiinae). *Records of the South Australian Museum* 21: 85–117.
- Pledge, NS. 1992. The Curramulka Local Fauna: a late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 9: 115–142.
- Rieppel, O. 1984. The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zoological Journal of the Linnean Society* 82: 291–318.
- Shea, GM. 1990. The genera *Tiliqua* and *Cyclodomorphus* (Lacertilia: Scincidae): generic diagnoses and systematic relationships. *Memoirs of the Queensland Museum* 29: 495–520.
- Shea, GM & Hutchinson, MN. 1992. A new species of lizard (*Tiliqua*) from the Miocene of Riversleigh, Queensland. *Memoirs of the Queensland Museum* 32: 303–310.
- Smith, MJ. 1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia IV. Reptiles. *Transactions of the Royal Society of South Australia* 100: 39–51.
- Sumida, S & Murphy, RW. 1987. Form and function of the tooth crown structure in gekkonoid lizards (Reptilia, Squamata, Gekkonidae). *Canadian Journal of Zoology* 65: 2886–2892.
- Tedford, RH, Wells, RT & Barghoorn, SF. 1992. Tirari Formation and contained faunas, Pliocene of the Lake Eyre Basin, South Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 9: 173–194.
- Wilkinson, J. 1995. Fossil record of a varanid from the Darling Downs, southeastern Queensland. *Memoirs of the Queensland Museum* 38: 92.
- Woods, JT. 1956. The skull of *Thylacoleo carnifex*. *Memoirs of the Queensland Museum* 13: 125–140.
- Woods, JT. 1960. Fossiliferous fluviatile and cave deposits. In D Hill (ed) 'The Geology of Queensland'. *Journal of the Geological Society of Australia* 7: 393–403.
- Woods, JT. 1962. Fossil marsupials and Cainozoic continental stratigraphy in Australia: a review. *Memoirs of the Queensland Museum* 14: 41–49.
- Wroe, S & Mackness, BS. 1998. Revision of the Pliocene dasyurid *Dasyurus dunmalli* (Dasyuridae, Marsupialia). *Memoirs of the Queensland Museum* 42: 605–612.
- Wroe, S & Mackness, BS. 2000a. Additional material of *Dasyurus dunmalli* from the Pliocene Chinchilla Local Fauna of southeastern Queensland and its phylogenetic implications. *Memoirs of the Queensland Museum* 45: 641–645.
- Wroe, S & Mackness, BS. 2000b. A new genus and species of dasyurid from the Pliocene Chinchilla Local Fauna of southeastern Queensland. *Alcheringa* 24: 319–326.

APPENDIX 1

Osteological material used for comparisons. Specimens are from the Herpetology Section of the South Australian Museum and the Western Australian Museum (WAM prefix).

Gekkonines

Christinus marmoratus (R35562; R39934), *Cosymbotus platyrus* (R36789), *Cyrtodactylus louisianensis* (R14002), *Gehyra australis* (R34136), *G. dubia* (R42872), *G. sp.* (2n = 44) (R44595), *G. catenata* (R35561), *G. oceanica* (R08687), *G. purpurascens* (R36377), *G. robusta* (R34222), *Gekko gecko* (R35559), *G. japonicus* (R07435), *G. vittatus* (R55978) *Gonatodes humeralis* (R40088), *Gymnodactylus darwini* (R40090), *Hemidactylus frenatus* (R35564), *Heteronotia binocci* (R09751 A, R33565, R39935), *Nactus cheverti* (R09740 B), *Paroedura picta* (R55105), *Phelsuma madagascariensis* (R40025), *Ptyodactylus hasselquisti* (R49804), *Tarentola annularis* (R40024), *Thecadactylus rapicauda* (R40099–100).

Diplodactylines

Bavayia ornata (R06752), *Crenadactylus ocellatus* (R03113 C), *Diplodactylus byrnei* (R13514), *D. conspicillatus* (R19967), *D. damaeus* (R20017, R24553) *D. 'granariensis'* (SA populations) (R02010, R26494, R29135), *D. immaculatus* (R42676), *D. pulcher* (R26383), *D. steindachneri* (R05153, R52746), *D. stenodactylus* (R07592, R21240, R26777), *D. tessellatus* (R03876, R40938), *D. vittatus* (R35568), *Hoplodactylus pacificus* (R11025), *Nephurus asper* (R35567), *N. laevis* (R00309 A, R27044–45), *N. milii* (R55422, R57083), *N. stellatus* (R32297), *Oedura lesueurii* (R33597), *O. marmorata* (R42893), *O. monilis* (R35563), *O. tryoni* (R33583), *Phyllurus platurus* (R35054), *Rhynchoedura ornata* (R35827), *Salvatorius swaini* (R29205), *Strophurus ciliaris* (R10697, R35566), *S. intermedius* (R14325 C).

A range of pygopod skulls was also examined (see Hutchinson 1997 for listing).

Egernia group skinks

Cornicia zebrata (R35765), *Cyclodomorphus maximus* (WAM R77193, WAM R77637), *C. michaeli* (R35682), *C. gerrardii* (R35761, R47699), *C. melanops elongatus* (R03231, R03856 G, R35681), *C. venustus* (R38021), *Egernia coventryi* (R35686, R47693–94), *E. cunninghami* (R35680, R35763), *E. depressa* (R03433 II), *E. formosa* (WAM R65803), *E. hosmeri* (R22510), *E. inornata* (R07234, R07238, R07245 A, R35687), *E. kingii* (WAM R36376, WAM R89269–70), *E. lucrosa* (WAM R36019), *E. major* (R27043, R35762), *E. multiscutata* (R08469, R25245), *E. napoleonis* (R35692, R51076, WAM R45350), *E. pilbarensis* (WAM R78945), *E. pulchra* (R40026, WAM R71884), *E. richardi* (R10841), *E. saxatilis intermedia* (R43961), *E. stokesii* (R02560, R41913), *E. striata* (R07179, R07198), *E. striolata* (R02909 B, R16593, R26891, R38019), *E. whitii* (R02726, R35690, R27042, R35689, R45316, R34886, R35688, R35691), *Tiliqua adelaidensis* (R40738, R40745, R43412), *T. gigas* (R11419), *T. multifasciata* (R27041, R35757), *T. nigrolutea* (R02725, R27048, R27050, R47698), *T. occipitalis* (R02724, R25369, R27047, R35758), *T. rugosa* (R02563[2], R02564, R27026, R27028, R02801, R25615, R27027, R27029, R27584, R31855, R35760), *T. scincoides* (R02561, R27036–40, R35759, R38020, R43962, R27094).

APPENDIX 2

TABLE 1. Measurements (mm) of ?*Megalania* dorsal vertebrae from Bluff Downs and Chinchilla Local Faunas compared with *Varanus giganteus*. Measurements as defined in Methods. Range (mean \pm standard deviation). Data for *V. giganteus* taken from Smith (1976), for Bluff Downs from Mackness & Hutchinson (2000).

Specimen	No	Pr-Po	BW/Pr-Po	CW/Pr-Po	Pr-Pr/Pr-Po
<i>V. giganteus</i>	20	24.5–27.1 (25.7 \pm 0.14)	0.54–0.64 (0.58 \pm .005)	0.55–0.63 (0.59 \pm .006)	0.88–1.01(0.92 \pm .007)
Bluff Downs	7	24.5–27.1 (25.7 \pm 0.14)	0.54–0.64 (0.58 \pm .005)	0.55–0.63 (0.59 \pm .006)	0.88–1.01(0.92 \pm .007)
Chinchilla	4	24.5–27.1 (25.7 \pm 0.14)	0.54–0.64 (0.58 \pm .005)	0.55–0.63 (0.59 \pm .006)	0.88–1.01(0.92 \pm .007)

TABLE 2. Measurements (mm) of individual ?*Megalania* vertebrae. Measurements as defined in Methods.

Specimen	Pr-Po	Pr-Pr	Po-Po	BW	CW	COW	CEL
WPC116	39.4	33.2	39.3	20.5	26.1	27.6	25.0
WPC2014	38.9	46.4	41.4	–	–	30.4	–
WPC2409	48.3	57.3	49.5	26.4	29.4	31.6	28.2
WPC3322	37.2	43.5	40.4	17.6	23.2	25.2	26.4
WPC3555	56.8	–	–	–	–	–	–
WPC3556	44.3	–	–	–	–	–	–
(Mean/SD)	(41.6 \pm 6.6)	(47.6 \pm 6.6)	(42.6 \pm 4.6)	(21.5 \pm 4.5)	(26.2 \pm 3.1)	(28.7 \pm 2.9)	(26.5 \pm 1.6)

TABLE 3. Measurements (mm) of centra of dorsal vertebra of fossil *Varanus* sp. from Chinchilla Local Fauna (WPC), Bluff Downs Local Fauna (QMF) and extant *Varanus varius* (AR7641).

Specimen	Measurement	Specimen	Measurement
WPC118	12.2	AR7641 (a)	15.3
WPC1430	16.5	AR7641 (b)	15.3
QM F7774	14.2	AR7641 (c)	15.4
QM F23238	10.5	AR7641 (d)	15.4
QM F23659	10.8	AR7641 (e)	15.6
QM F23683	13.8	AR7641 (f)	15.7

TABLE 4. Comparison of lizard taxa recovered from the Queensland Pliocene (Chinchilla and Bluff Downs Local Faunas. Source: Mackness & Hutchinson 2000). Code: present •, absent x, endemic form ^(e).

Taxa	Chinchilla	Bluff Downs
Gekkonidae		
cf <i>Heteronotia</i>	x	•
<i>Diplodactylus</i>	• ^(e)	x
Agamidae		
unidentified material	•	•
Varanidae		
? <i>Megalania</i>	•	•
<i>Varanus</i>	•	•
Scincidae		
<i>Tiliqua</i>	• ^(e)	•
<i>Cyclodomorphus</i>	•	x
<i>Egernia</i>	x	•
<i>Eulamprus</i>	x	•